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NICHE SEPARATION AND COMPETITIVE COEXISTENCE IN MYCOPHAGOUS *DROSOPHILA* (DIPTERA: DROSOPHILIDAE)

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Abstract.—Four species of mycophagous *Drosophila* whose larvae experience food limitation in nature overlap broadly in their utilization of various mushroom species. Interspecific competition is intensified by the presence of other Diptera in mushrooms, by the attractiveness of particular mushrooms for *Drosophila*, and by a preference of two of the *Drosophila* species with slow development for older, more crowded mushrooms. Competitive exclusion should be slowed by the large fluctuations in population sizes of these flies, and also prevented by interspecific differences in host use. Variation in host use results from differences among fly species in habitat occurrence, host preferences by ovipositing females, and the suitability of various resources for larval development.

Among *Drosophila*, mycophagous species are especially suitable for ecological study since they are diverse and usually abundant, their larval feeding sites are discrete, and they must contend with a suite of sometimes harsh selection pressures imposed by their mushroom hosts. Although mushrooms vary in the physiological challenges they present to flies, specialization upon individual species would seem difficult since mushrooms are both spatially and temporally unpredictable in occurrence. This is because fructification is dependent on suitable rainfall, temperature, and edaphic conditions (Wilkens and Harris, 1946; Shorrocks and Charlesworth, 1980), and because the fruiting bodies themselves are so ephemeral. It is not surprising, then, that the common mycophagous drosophilids of the northeastern United States—*Drosophila falleni* Wheeler, *D. recens* Wheeler, *D. putrida* Sturtevant, *D. testacea* Roser—are polyphagous, each species having been bred from 10 to 20 genera of fleshy fungi (reviewed in Grimaldi, 1983). In contrast, *Mycodrosophila claytonae* Wheeler and Takada and *Drosophila duncani* Sturtevant in the United States and *D. phalerata* Meigen in England specialize on fungi that are particularly long-lasting and thus more predictable in occurrence (Shorrocks and Charlesworth, 1980, 1982; Lacy, 1984).

Given the facts that (1) mushrooms are unpredictable resources; (2) mycophagous drosophilids overlap broadly in the species of mushrooms they use as breeding sites as a result of their polyphagy; and (3) the four common mycophagous *Drosophila* of the Northeast often occur sympatrically, then one might conclude that these species rarely if ever experience food shortages. This interpretation, however, is not supported by the facts.

In a previous study (Grimaldi and Jaenike, 1984) it was shown that mushrooms occurring in the field are in limited supply for *Drosophila falleni, D. recens, D.*

putrida and *D. testacea* and for two other Diptera, the cranefly *Limonia triocellata* (Osten Sacken) (Tipulidae) and the woodgnat *Sylvicola alternatus* (Say) (Anisopodidae). Mushrooms were separated into halves, to one half of each more mushroom was added in order to release larvae from competition for food. Pairwise comparisons of halves for each mushroom revealed that mortality and sizes of flies bred from them were adversely affected in the control (unsupplemented) halves. Although the experimental design could not distinguish between the effects of conspecifics or not, it is very likely that both intraspecific and interspecific competition occurred.

Host use was compared for *Drosophila falleni, D. recens, D. putrida,* and *D. testacea* based on breeding records and inferences made from other characteristics. Presumably, trophic morphologies, such as egg and larval mouthpart shapes are associated intimately with the types of breeding site (Okada, 1963; Kambysellis and Heed, 1971). The habitats and seasons in which *Drosophila* occur determine which hosts flies can encounter. Since larvae are not vagile and because oviposition is generally restricted to fewer hosts than the number that larvae can actually use (Kearney, 1982), oviposition site preference is another ecologically important trait in *Drosophila*. Although their coexistence may result from a balance between the rates of migration and local competitive exclusion (Horn and MacArthur, 1972; Atkinson and Shorrocks, 1981; Kneidel, 1983), the ecological differences documented here among the four *Drosophila* species are probably important in allowing their coexistence during competition.

METHODS

Most field portions of the study were conducted from the spring through early fall of 1981 and 1982 at Chenango Valley State Park, the SUNY Binghamton Nature Preserve, and a site in Vestal, New York. *Drosophila* were reared from various field-collected substrates on top of moist sand and leaf litter in various gauze-covered containers. Lab portions of the study used flies raised on commercial mushroom, *Agaricus bisporus. Drosophila testacea* was difficult to rear because a strongly female-biased sex ratio became established in lab populations. Therefore, it was not used in tests of oviposition preference and in most larval development comparisons. Adult size was determined by measuring the length from the anterior thorax to the posterior tip of the scutellum at 30× magnification with an ocular micrometer. All measured flies were first preserved in 70% ethanol.

Trophic morphologies.—Larval mouthpart structure and egg morphology were compared for *Drosophila falleni, D. recens, D. testacea,* and *D. putrida* and some non-mycophagous species that were chosen for their ease in culturing, phylogenetic relationships, and breeding sites. Only newly laid eggs and third instar larval mouthparts were used. Mouthparts were first dissected from larvae and adhering tissue cleared away in hot 10% KOH.

Larval development.—Larvae were raised on two-gram pieces of mushroom. Three females per vial were first allowed to oviposit for 24 hours on each piece, then removed.

Development time for the four mycophagous species was determined in two trials. Trial one measured time from egg to eclosion on three different substrates: frozen and fresh *Agaricus bisporus,* and frozen *Amanita muscaria.* Nine replicates per substrate were made for each species except *D. testacea,* which could not be grown. Since only small differences for substrate effects were found in *D. recens*, the results for all three substrates were combined. Trial two measured the time from egg to pupation and to eclosion on only fresh *Agaricus*. Twelve replicates for each of the four species were set up in trial two, but only *D. falleni* was viable in all of them. Some *D. testacea* cultures were also used here. Development time was measured as $\sum_{i=1}^{n}$ (% flies developed) (day number) for each vial. An ANOVA for unequal N, done within trials only, compared development times among species.

Abilities of larvae of three of the mycophagous species to subsist on three commonly used fungus hosts at three temperatures were compared. Adult size was used as an indicator of how well larvae developed. *Amanita muscaria* was chosen as one rearing substrate since it is soft, deliquesces with age, and contains toxins (Wieland, 1968). *Russula compacta* has denser tissue, decays slower, and contains no known toxins. *Polyporus squamosus*, a very distinctive host, is leathery, decays slowest, and also has no known toxins. Fifteen, 21, and 27°C were chosen as representatives of the range of temperatures to which larvae are exposed in nature. There were three replicates per treatment. From each treatment 20 males and 20 females (if available) were pooled and measured. A 2-way ANOVA for unequal N tested for the main effects of temperature and substrate and for any interactions. Duncan's multiple range test delimited pairs of similar treatment effects for each species (Sokal and Rohlf, 1969).

Population size: seasonal and habitat variation.—A constant-effort trapping technique, using the trap in Fig. 1, assessed phenology. Each trap, suspended 1.5 m from the ground, was baited with equal amounts of whole banana mashed with yeast and smeared to the walls of the upper chamber. The trap was designed so that flies would enter the black bottom chamber, become attracted to the bait and light from the top chamber and fly into it. Since escape of the flies is limited by the small hole in the mesh cone, flies would accumulate in the upper chamber of the trap during the six-day trapping period. Between two and four traps were used at each sampling. Population size during a trapping period was denoted as the mean number of flies per trap in each of the two study sites. No statistics were done on the data; comparisons were made visually on plotted trends for the presence of any numerical changes.

Flies were trapped in three different locations in the eastern United States to see if species separated by altitude or forest type at each location. The geographic locations and collection periods were Mount Desert Isle, ME from 29 June to 1 July 1982, the Great Smoky Mountains National Park, TN from 18 July to 23 July 1982 (J. Jaenike, collector), and East Charleston, VT from 18 July to 27 July 1982. At each location a high elevation/coniferous forest site and a low elevation/deciduous forest site were sampled (for details of each site, see Grimaldi, 1983). Bait was always mushroom, sometimes mixed with bananas or tomatoes (but always the same between sites at each location), which was then kept out for five days and sampled intermittently. Flies were pooled according to habitat and collecting period. A chi-square test was used to examine differences in species distribution.

Oviposition site preference (OSP).—Possible differences in the use of rotted

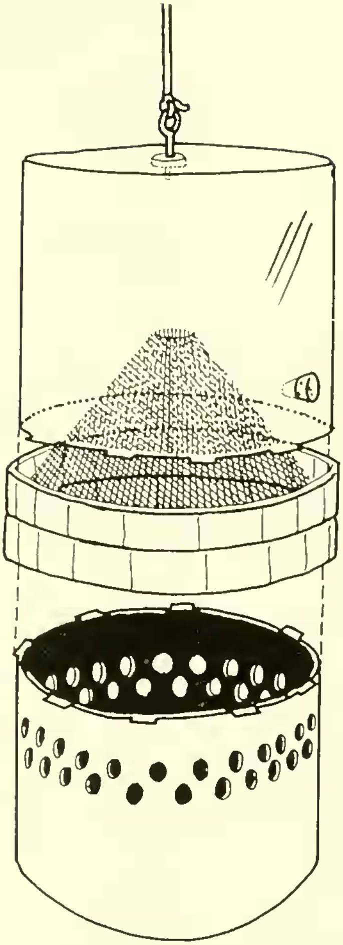

Fig. 1. *Drosophila* trap used to monitor population sizes.

versus fresh mushrooms were examined for the four mycophagous species. Seven rotted and nine fresh *Amanita* mushrooms growing in close proximity to each other were found at the SUNY Binghamton Nature Preserve (New York: Vestal, Broome County) on 21 July 1981. *Drosophila* adults on them were netted, identified, and counted. Since the mushroom surfaces had eggs on them, I assume that attractiveness to various *Amanita* is directly related to where the females oviposit (i.e. Fellows and Heed, 1971 for cactiphilic *Drosophila*).

The effects of host composition on OSP in *D. falleni, D. recens, D. putrida,* and also *D. immigrans* (a fruit breeder) were compared. Three mushroom and two plant substrates were prepared by blending each with water and agar, heating the mixture to 70°C, pouring it into test tubes and slicing equal sized plugs from each mold when the substance had solidified. The homogenization reduced the large variation in OSP found when unadulterated substrate pieces were offered because of differences in piece sizes, texture, and shape. The substrates used were *Amanita muscaria* (a toxic agaric with mild smell), *Russula compacta* (a nontoxic, fishy-

Table 1. Number of Diptera reared from mushrooms.

	Amanita				*Russula*				
	Chenango Valley		Vestal		Chenango Valley		Vestal		
	1981	1982	1981	1982*	1981*	1982	1981	1982	Total
Drosophila	276	523	1314	—	—	567	406	36	3122
Limonia	0	0	0	—	—	84	0	34	118
Sylvicola	0	0	0	—	—	268	0	0	268
Megaselia	0	501	0	—	—	0	0	0	501
Bradysia	0	0	0	—	—	0	0	122	122
Mycetophila	0	47	0	—	—	11	0	0	58

* *Amanita* or *Russula* mushrooms were not collected.

smelling agaric), *Leccinum scabrum* (a fruity-smelling bolete), skunk cabbage (*Symplocarpus foetidus*, a common aroid in which drosophilids breed), and lettuce (*Lactuca sativa*, a representative inocuous plant). Oviposition plugs were systematically arranged on the periphery of 8–10 large petri dishes per *Drosophila* species in which 100–150 adults were allowed to oviposit. An ANOVA and Newman-Keuls test (Sokal and Rohlf, 1969) on proportions of eggs laid on each substrate were used to rank OSP of each *Drosophila* species. Except for *D. putrida*, there were two OSP trials per species. Details of the experimental procedure are described elsewhere (Jaenike and Grimaldi, 1983).

RESULTS

Trophic morphology and breeding sites.—In total, 21 species of Diptera belonging to 11 families were reared from 54 mushrooms. There were 24 *Amanita*, 25 *Russula*, 2 *Cortinarius*, and 3 *Entoloma* mushrooms collected. *Drosophila* were the most common flies, and outnumbered all others 2:1 in *Russula* and 4:1 in *Amanita* (Table 1). *Bradysia* (Sciaridae) and *Megaselia* (Phoridae) were probably less important competitors for *Drosophila* than other flies since they are small and occured in only several mushrooms in large numbers. *Limonia triocellata* and *Sylvicola alternatus*, however, are not only much larger than *Drosophila*, but are fairly abundant in *Russula*. No *Limonia* or *Sylvicola* were reared from *Amanita*.

Major differences in breeding sites were found among some mycophagous *Drosophila* species and were best reflected by differences in mouthpart structure. Of

Table 2. Drosophilidae bred from various mushrooms (N = 34) and from skunk cabbage plants, *Symplocarpus foetidus* (N = 92) at Chenango Valley, N.Y. in 1982.

	Host: Numbers Bred	
	Mushrooms	*Symplocarpus*
Drosophila falleni	559	9
D. recens	78	146
D. putrida	182	10
D. testacea	334	0
Scaptomyza graminum	1	522

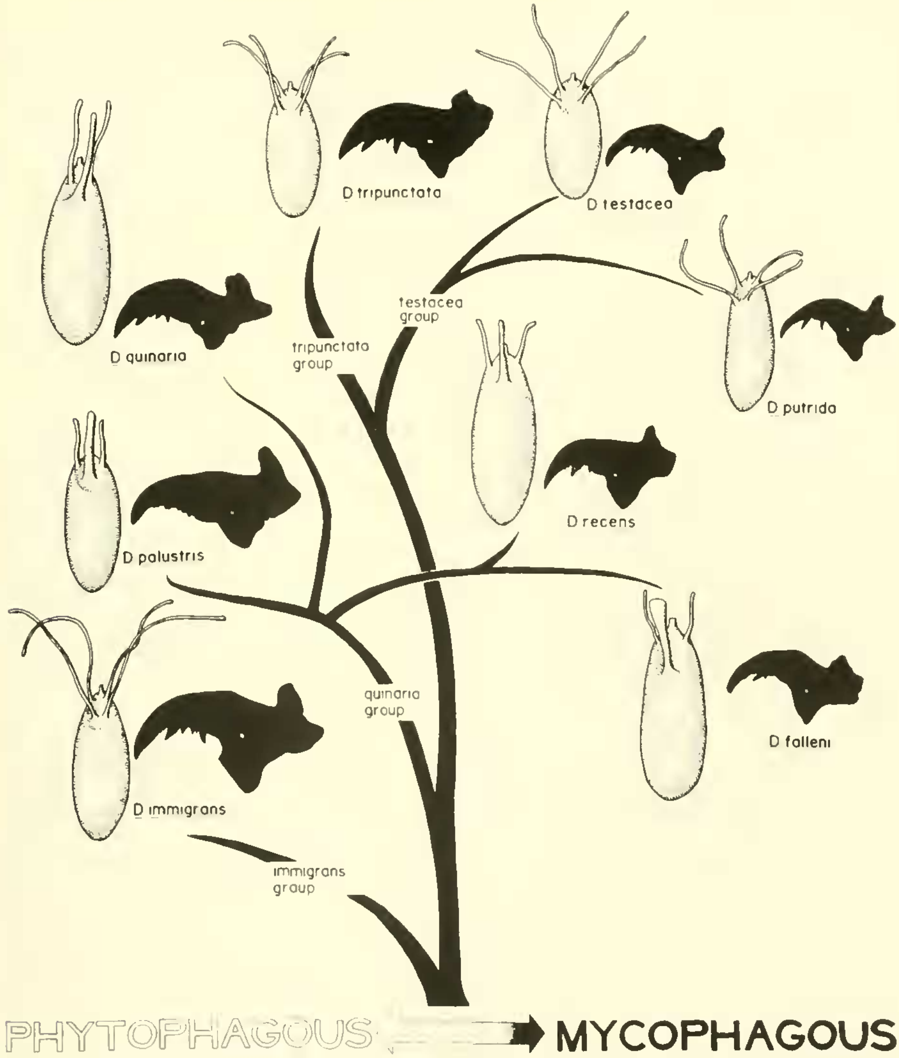

Fig. 2. Eggs and third instar larval mouthparts of 8 *Drosophila* species arranged according to breeding sites (position along the horizontal axis) and phylogenetic relationships. Phylogeny is from Throckmorton (1975).

the flies bred from mushrooms and from skunk cabbage, *D. recens* was least host restricted (Table 2). Data on *Scaptomyza graminum* (Fallén) (Drosophilidae), the most common fly on *Symplocarpus*, is presented for comparison. The stem and leaf breeding species, such as *D. quinaria* and *D. palustris* (Spencer, 1942) had heavy mouthparts with little curvature and seems to reflect the condition found in several Hawaiian leaf-breeding species (Mangan, 1978). Mycophages, however, had strongly curved, thin mouthparts (Fig. 2). Fruit breeders (*D. immigrans*) resemble mycophages more than leaf breeders in this respect, perhaps because of a similarity in breeding site texture. *Drosophila recens* and *D. tripunctata* Loew, the latter of which has been bred from fruits (Sturtevant, 1921), many different

Table 3. *Drosophila* development time, in days.

Drosophila	Trial	Number of Replicates	Mean (± SE) Time from Egg to	
			Pupation	Eclosion
D. falleni	1	27	—	14.2 ± .12^a
	2	12	7.2 ± .09^b	13.8 ± .07
D. recens	1	27	—	14.2 ± .08^a
	2	11	7.3 ± .06^b	14.1 ± .05
D. putrida	1	27	—	15.8 ± .23
	2	7	8.9 ± .33^c	15.8 ± .26
D. testacea	1	—	—	—
	2	4	8.6 ± .26^c	15.4 ± .19

Superscript letters denote values which are not significantly different ($P > .1$, ANOVA). Comparisons are within trials only.

mushrooms (Lacy, 1984), and even slug carcasses (Kneidel, 1983), had intermediately-shaped mouthparts.

Although the chorion and filaments of eggs function in respiration (Hinton, 1981), there was no obvious relation between egg size, egg shape, filament number or length and the type of breeding site. Variations in egg morphology among these species reflected phylogenetic relationships (cf. Throckmorton, 1962, 1966), not ecological habits.

Table 4. Effects of temperature and mushroom on *Drosophila* sizes. Size is thorax length measured in ocular units (1.0 ocular unit = .38 mm).

Species	Sex	Source of Variation	F	Variables Mean Sizes†					
				15°	21°	27°	*Amanita*	*Russula*	*Polyporus*
D. falleni	M	Temperature	34.25***	2.86	2.91	2.59			
		Mushroom	28.92***				2.94	2.75	2.65
		Temp × Mush	4.14**						
	F	Temperature	56.86***	3.25	3.25	2.80			
		Mushroom	29.88***				3.32	2.99	3.08
		Temp × Mush	12.12***						
D. recens	M	Temperature	69.07***	2.94	2.96	2.69			
		Mushroom	27.16***				2.95	2.84	2.74
		Temp × Mush	5.44***						
	F	Temperature	20.14***	3.20	3.18	2.96			
		Mushroom	2.72*				3.22	3.12	3.08
		Temp × Mush	.66						
D. putrida	M	Temperature	50.74***	2.20	2.33	2.02			
		Mushroom	8.13***				2.24	2.19	2.12
		Temp × Mush	6.79***						
	F	Temperature	50.10***	2.58	2.72	2.40			
		Mushroom	15.51***				2.67	2.49	2.55
		Temp × Mush	.73						

† Values underlined are not significantly different ($P > .05$, Duncans' multiple range test). Comparisons are within treatment groups only for each species.

* $P \leq .05$; ** $P \leq .01$; *** $P \leq .001$; df for treatment = 2.

Table 5. Habitat occurrence in coexisting *Drosophila*.

Location, Species	Number of Flies High Elevations Coniferous Forests	Low Elevations/ Deciduous Forests
Deer Isle, Maine		
Drosophila falleni	247	183
D. recens	139	53
D. putrida	68	48
D. testacea	83	188
East Charleston, Vermont: Mad Brook Farm		
D. recens	15	0
D. testacea	32	11
East Charleston, Vermont: Bald Mountain		
D. testacea	9	25
Great Smoky Mountains National Park, Tennessee		
D. testacea	18	14
D. recens	57	5

Larval development.—In the lab, *D. falleni* and *D. recens* had egg to adult development times about one day shorter than either *D. testacea* or *D. putrida* (Table 3). Closely related species pairs were not significantly different in this respect ($P > .10$, ANOVA).

Drosophila falleni, D. recens and *D. putrida* are easily raised on commercial mushroom in the lab, in contrast to the difficulty I had rearing them on standard *Drosophila* media. Different mushroom species were not equally suitable for each species and temperature differences accentuated the effects. Flies of each species reared as larvae on *Amanita muscaria* were always largest (Table 4). Suitability of *Russula compacta* and *Polyporus squamosus* varied between species and sexes. For each species, larval development at 27°C resulted in adult stunting, but the temperature which maximized fly size varied. *Drosophila falleni* and *D. recens* did equally well at 15°C and 21°C, but *D. putrida* grew largest at 21°C. The combined effects of temperature and substrate were important for four of the six species-sex groups. *Drosophila falleni* and *D. recens* males, for instance, were smallest when raised on *Polyporus* at 27°C than any other treatment.

Species abundance.—*Drosophila* were not abundant at all of the locations that were sampled, even though the trapping periods coincided (Table 5). However, *D. recens* and *D. testacea* were abundant enough at each location to show that the former occurred most at high elevations and in coniferous forests. *Drosophila testacea* showed no consistent distribution. At the Deer Isle location, however, closely related species pairs had separate distributions: *D. falleni* had no obvious habitat association, but 72% of the *D. recens* were captured in a fir forest ($\chi^2 = 24.02$, $P < .01$). Also, *D. putrida* was relatively more abundant than *D. testacea* in the fir forest ($\chi^2 = 22.06$, $P < .01$). In the Great Smoky Mountains, Lacy (1984) too found *D. recens* to be more abundant at higher elevations.

In New York, populations of the two *quinaria*-group species and two *testacea*-group species separated somewhat by season (Fig. 3). *Drosophila testacea* and *D. putrida* were more common in the fall, but the other two species were equally

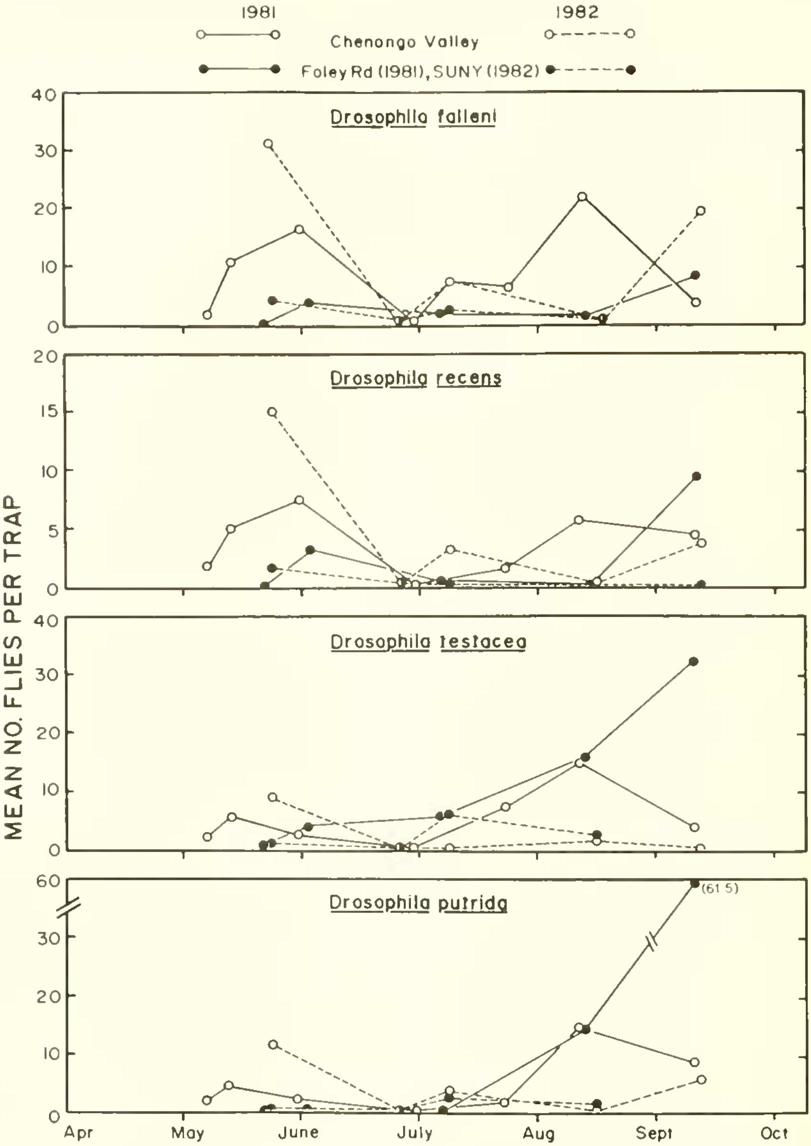

Fig. 3. Relative seasonal abundance of 4 coexisting *Drosophila* species based on constant-effort trapping during 2 years.

abundant in the spring and fall. A striking similarity to each was the simultaneous population crash in late June. This suggests that probably two generations occurred per year: a spring generation that used early mushrooms (i.e. *Polyporus squamosus* and *Tricholomopsis platyphylla*) and a late summer-early fall generation that bred in the more abundant, diverse flora found then (Grimaldi, 1983).

Oviposition site preference.—Based on the lab OSP tests, the mycophagous species preferred mushrooms over plant substrates and the fruit breeder, *D. immigrans,* preferred plant substrates (Fig. 4). Results were highly repeatable between

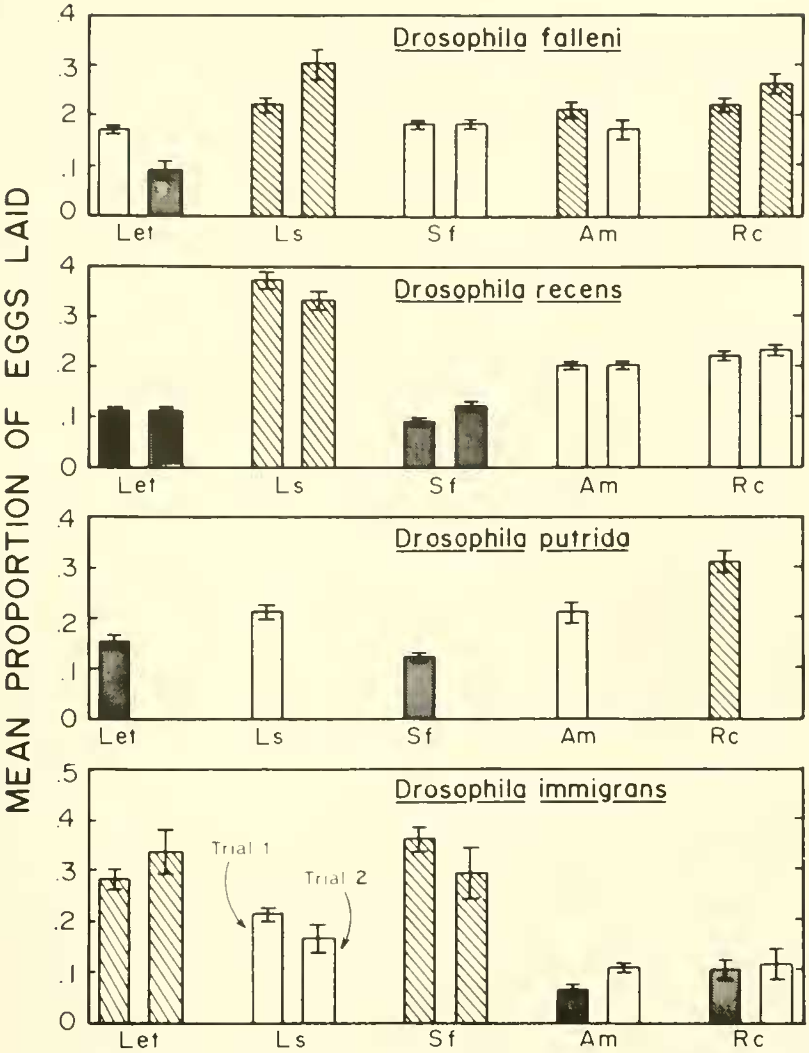

Fig. 4. Oviposition site preferences of 4 *Drosophila* species for 5 substrates. Substrates are lettuce (Let), *Leccinum scabrum* (Ls), *Symplocarpus foetidus* (Sf), *Amanita muscaria* (Am), and *Russula compacta* (Rc). The left bar of each pair represents trial 1. Bars with the same shading, within a trial and species only, denote hosts which were equally preferred (Newman-Keuls test, $P \leq .05$).

trials, with a mean of 380 eggs laid per oviposition dish. However, the OSP for particular mushrooms varied among the mycophagous species: *D. falleni* preferred *Leccinum* and *Russula*, *D. recens* preferred *Leccinum*, and *D. putrida* preferred *Russula*. *Drosophila recens* did not have a preference for *Symplocarpus* greater than the other mycophagous species. Also, *Amanita* was consistently the least preferred mushroom for each species.

The *Drosophila* netted over rotted and fresh *Amanita* at SUNY preferred the rotted ones (Table 6). This preference was accentuated in *D. testacea* and *D. putrida* ($\chi^2 = 37$, $P < .01$). Kimura (1980) noted *D. testacea* in Japan also preferred ovipositing on decaying versus fresh mushrooms.

Table 6. Numbers of *Drosophila* caught on rotted and fresh *Amanita* mushrooms.

Drosophila Species	Rotted (N = 7)	Fresh (N = 9)
D. falleni	81 (57%)	62 (43%)
D. recens	33 (67%)	16 (33%)
D. putrida	25 (96%)	1 (4%)
D. testacea	48 (98%)	1 (2%)
Total	187 (70%)	80 (30%)

DISCUSSION

Drosophila were the most abundant Diptera in mushrooms and are, therefore, likely to compete most with each other. Other flies, such as *Sylvicola* and *Limonia*, probably also compete with *Drosophila* for mushroom food, but only in some of the mushrooms used by *Drosophila*. Accordingly, there is substantial ecological separation between the four *Drosophila* species commonly found together in mushrooms.

Several facts implicate that the food for which these mycophagous *Drosophila* larvae probably compete is mushroom tissue, not just the yeasts and bacteria growing in it. First, mushroom tissue is a complete and generally nutritious insect diet (Martin, 1979). Also, several mycophagous *Drosophila* species are tolerant to naturally high levels of the mushroom toxin, α-amanitin (Jaenike et al., 1983). Thus, unlike for a cactiphilic species (Fogelman et al., 1981), these larvae are unlikely to partition their food by selective foraging on patches of certain microorganisms.

Drosophila recens is facultatively mycophagous; the other three species are strictly mushroom breeders. In addition, species-group differences were apparent: *D. testacea* and *D. putrida* had development times longer than those of *D. falleni* and *D. recens* and adults are attracted to older, decaying mushrooms. It has been inferred from electrophoresis that for *D. falleni*, but not the other three species, up to 60 sibs, the progeny of one female, can be found in a single *Amanita* (Grimaldi, 1983). This evidence strongly suggests that female *D. testacea* and *D. putrida* oviposit on mushrooms already inhabited by larvae and thus put their offspring at a disadvantage in scramble competition with the *quinaria*-group flies.

The field experiment mentioned earlier corroborates that *D. putrida*, but not *D. testacea*, is under harsh competitive pressure (Grimaldi and Jaenike, 1984). In that experiment, the reduction of "fitness" (a function of survivorship and female fecundity) due to competition for mushroom food was approximately 60% for *D. putrida*, 25 and 30% for *D. testacea* and *D. falleni*, and only 15% for *D. recens*. This is opposite of what one might expect based on the assumption that competition should affect resource use. *Drosophila recens* is the most polyphagous species, but probably not because of competitive pressure. *D. putrida*, on the other hand, was affected most by competition but shows little evidence of niche separation from the other *Drosophila*.

What prevents poor competitors like *D. putrida* from being excluded from the mycophagous niche? My results suggest that at least six factors can explain this competitive coexistence.

1.—Mushrooms are a heterogeneous insect diet. Their texture ranges from woody to almost liquid and many species are known to contain a variety of toxins. Depending on the host mushroom, slight develomental advantages can be conferred on a particular *Drosophila* species that make it less susceptible to the effects of competition. The effects of different breeding substrates on competitive outcomes in lab populations of *Drosophila* has been shown elsewhere (Merrell, 1951; Fellows and Heed, 1972; Mangan, 1982).

2.—Fluctuating competitive asymmetries resulting from different hosts can be enhanced by microclimatic variations such as temperature. For example, *D. putrida* would probably not compete well with *D. falleni* at 15°C since it develops slowly at this temperature. Three species of *Drosophila* in the *affinis* subgroup have competitive abilities affected by temperature (Fogelman and Wallace, 1980).

3.—Closely related species of mycophagous *Drosophila* can segregate by association with particular habitats. Since altitude and forest type influence species abundance, separation of the four species by habitat can be particularly important at northern latitudes and along the Appalachian Mountains.

4.—*Drosophila putrida* (and probably also *D. testacea*) are not as cold-adapted as *D. falleni* and *D. recens*. This is one reason why *D. putrida* and *D. testacea* are relatively more abundant in the late summer and early fall when temperatures are generally warmer. Seasonal separation is also known to occur in several other mycophagous *Drosophila* in England (Shorrocks and Charlesworth, 1980).

5.—Close populational tracking of resources is prevented by patchy mushroom distribution. The resulting population fluctuations, although reflecting resource supply, do not allow population size to equilibrate at high levels, which might favor only competitive ability.

6.—Although three of the four *Drosophila* are obligately mycophagous, differences in host preference that were observed in the lab can become apparent during periods when the standing mushroom crop is diverse and abundant, as in the early fall. Such periods of mushroom "bloom" should also provide the resources for a major proportion of the yearly *Drosophila* population. Differences in breeding records among some sympatric mycophagous *Drosophila* have been investigated for several faunas (Kimura, 1980; Shorrocks and Charlesworth, 1980; Lacy, 1984).

The saturated niche packing often seen in insect communities associated with ephemeral, unpredictable resources such as carrion (Beaver, 1977; Anderson, 1982), dung (Hanski and Koskela, 1977; Peck and Forsyth, 1982), and fungi (Buxton, 1960; Hackman and Meinander, 1979) is explainable even if competition is severe. Exclusion by a dominant competitor usually is prevented by seasonal, habitat, and successional separation of species, but probably also by fluctuations in competitive ability concomitant with diet and microclimatic variations.

All being equal, it is possible that just a sufficiently high variance in the distribution of "fugitive" competitors on the limiting resource can explain coexistence. However, as one model shows (Atkinson and Shorrocks, 1981), the idea suffers from some assumptions that are unrealistic. For example, identical competitors would coexist if they are not contagiously distributed and if individual breeding sites support only a few flies. Almost all work on flies that utilize transient breeding sites, including this study, shows these assumptions not to be the case. Hymenopterous parasitoids account for up to 3% of the larval mortality in mycophagous *Drosophila* (Grimaldi, 1983), and *Howardula aoronymphium* (Allantonematidae: Nematoda) can infest and kill up to 20% of the adults (Montague and Jaenike, 1985). Predation, relative resource separation, and competitive asymmetries that constantly fluctuate are thus major factors maintaining the coexistence of insect competitors.

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